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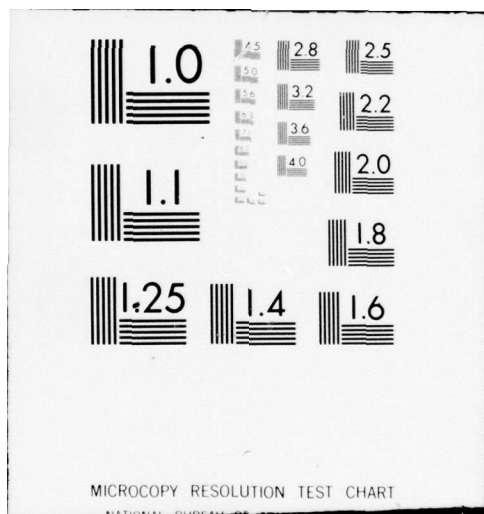
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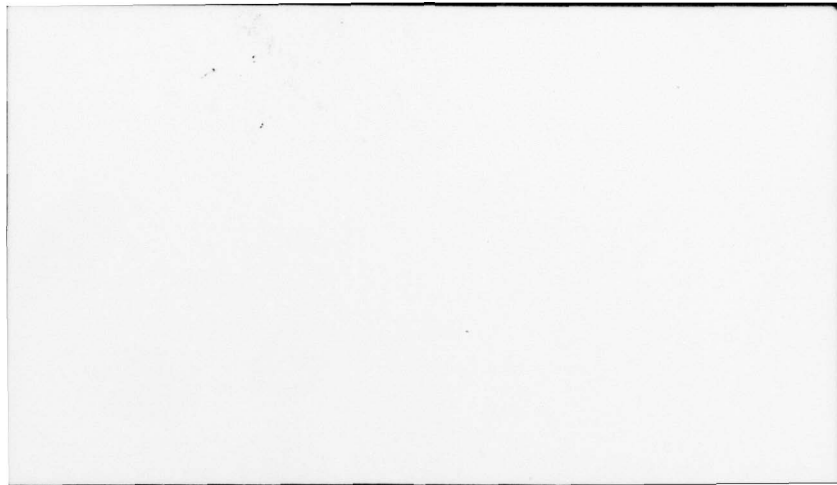
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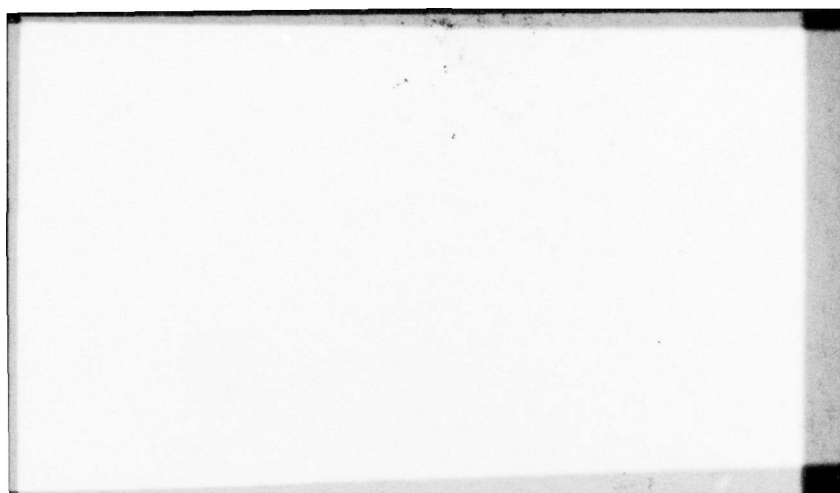
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6 A FACILITATION EFFECT IN
ORIENTATION DISCRIMINATION.

by

10 John Lott/Brown and
Iris M./Kortela

12 28 p.

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ABSTRACT

The minimal stimulus for orientation discrimination consists of two spots of light which define the orientation of an imaginary line. Luminance thresholds for discrimination of orientation were measured with two 5-min test spots, separated by 10, 20, 30 or 40 min of arc, located approximately 2 deg from the fovea. Test flashes were of 2-msec duration and varied in temporal relation from simultaneity to nearly 0.5 sec asynchrony. When measurements were made by an ascending method of limits with both test flashes increasing together, luminance thresholds for orientation discrimination were close to light detection thresholds and were uninfluenced by the temporal relation. When one of the flashes was presented by a constant luminance 0.6 log unit above detection threshold and the luminance of the other was the dependent variable, the luminance threshold for discrimination of orientation of the two spots varied with their temporal and spatial relations. For 30 min separation it was approximately 0.4 log unit below light detection threshold when the variable luminance spot preceded the fixed luminance spot by about 140 msec for each of two observers. Results with haploscopic presentation suggest that the effect may represent facilitation at the cortex.

INTRODUCTION

Interaction effects in the nervous system, both excitatory and inhibitory, play an important role in the processing of incoming information from peripheral sensory mechanisms. The organization of receptive fields in the retina, with excitatory centers and inhibitory surrounds or the converse, is frequently invoked in the explanation of the perceptual sharpening of contours and such contrast phenomena as Mach Bands, the Hermann grid and other contour effects (Ratliff, 1965; Jung, 1973). In an interesting series of papers, Westheimer (1965, 1967, Westheimer and Wiley, 1970) has demonstrated influences of the nature of stimulation of the surrounding region on thresholds for discrimination of a small retinal test field. His results are frequently explained on the basis of lateral inhibition effects.

It would seem possible to study interactions between two retinal locations most precisely by the use of two small stimulus spots, the temporal as well as the spatial relations of which can be carefully controlled. The time course of lateral excitatory and inhibitory processes in the retina could presumably be investigated by variation in the temporal relations of the stimuli for various spatial separations. Such a stimulus situation has been of interest as a possible method for direct electrophysiological investigation of retinal mechanisms, but it has not been used successfully. Some of the experiments associated with the general classification of metacontrast may be relevant, but most such experiments have employed relatively large stimulus regions and the criterion of effect has been assessed in terms of the brightness of the stimulus rather than detection threshold. Smith and Richards (1969) demonstrated interactions between line stimuli on the retina which could apparently be explained in terms of lateral interactions of measureable velocity, but these effects were best demonstrated with stimulus decrements rather than increments.

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Beitel (1936) has reported both inhibition and facilitation of the detection of a retinal test flash depending on the luminance and spatial separation of a conditioning flash of the same size.

The experiment reported here is the outgrowth of a series of earlier pilot investigations which were intended to explore further the possibility of studying retinal interaction processes psychophysically. It was hoped that stimulus conditions might be found which would reveal excitation and inhibition effects in human subjects and at the same time provide a basis for investigating retinal mechanisms which might underlie such effects in electrophysiological studies of animals. In our initial investigations, two small circular spots of approximately five-minute diameter were flashed at various spatial and temporal separations and subjects were requested to indicate when they appeared as separate. This discrimination became extremely difficult when the spot centers were separated by less than ten or fifteen minutes of arc. It was necessary to establish an objective criterion of threshold in order to achieve any reliability of response. The ascending method of limits was used with the requirement that subjects discriminate the relative positions of the two test spots as horizontal or vertical. Under these circumstances, in order to respond correctly, subjects must discriminate each of the two points of stimulation. There can not be complete summation of the two stimuli without loss of their individual identities. At the same time, the two points of stimulation may conceivably act mutually to excite or inhibit each other. Thus, one might expect a variation in threshold for orientation discrimination with variation in temporal or spatial separation of the stimuli.

In a pilot experiment, two test flashes were presented, each at the same luminance level below its light detection threshold. Luminance threshold

for discrimination of the orientation of the two spots was then determined in an ascending method of limits series. The two circular test spots were five minutes of arc in diameter, located approximately two degrees from the center of the fovea and separated spatially by from ten to twenty-five minutes of arc, measured from center to center. Temporal asynchronies were from zero to 240 msec. Thresholds were determined for each of four spatial separations and five onset asynchronies for each of two subjects. There were not significant systematic effects of changing either spatial or temporal separation of the test spots over the ranges investigated for either of the two subjects. Apparently, under the conditions of this experiment, no interaction effects, either excitatory or inhibitory, had any influence on the results with the stimulus parameters employed. These results have been presented in an earlier report (Kortela, 1975).

In the present experiment a procedure similar to that employed by Beitel (1936) was employed in which one of the test flashes was always presented at a suprathreshold level and the other in an ascending series. Under these conditions, significant effects of both spatial and temporal separation of the stimulus spots were found for each of two subjects, but it is unlikely that these effects are dependent upon retinal mechanisms.

APPARATUS

The optical system employed consisted of four channels for the presentation of a Maxwellian view of stimulus fields, the spatial and temporal relations among which could be controlled over a fairly wide range (Figure 1). Light from all four channels could be presented to the right eye of the observer. Two of the channels, C and D, could be presented either to the right eye or to the left eye. Channels A, B and

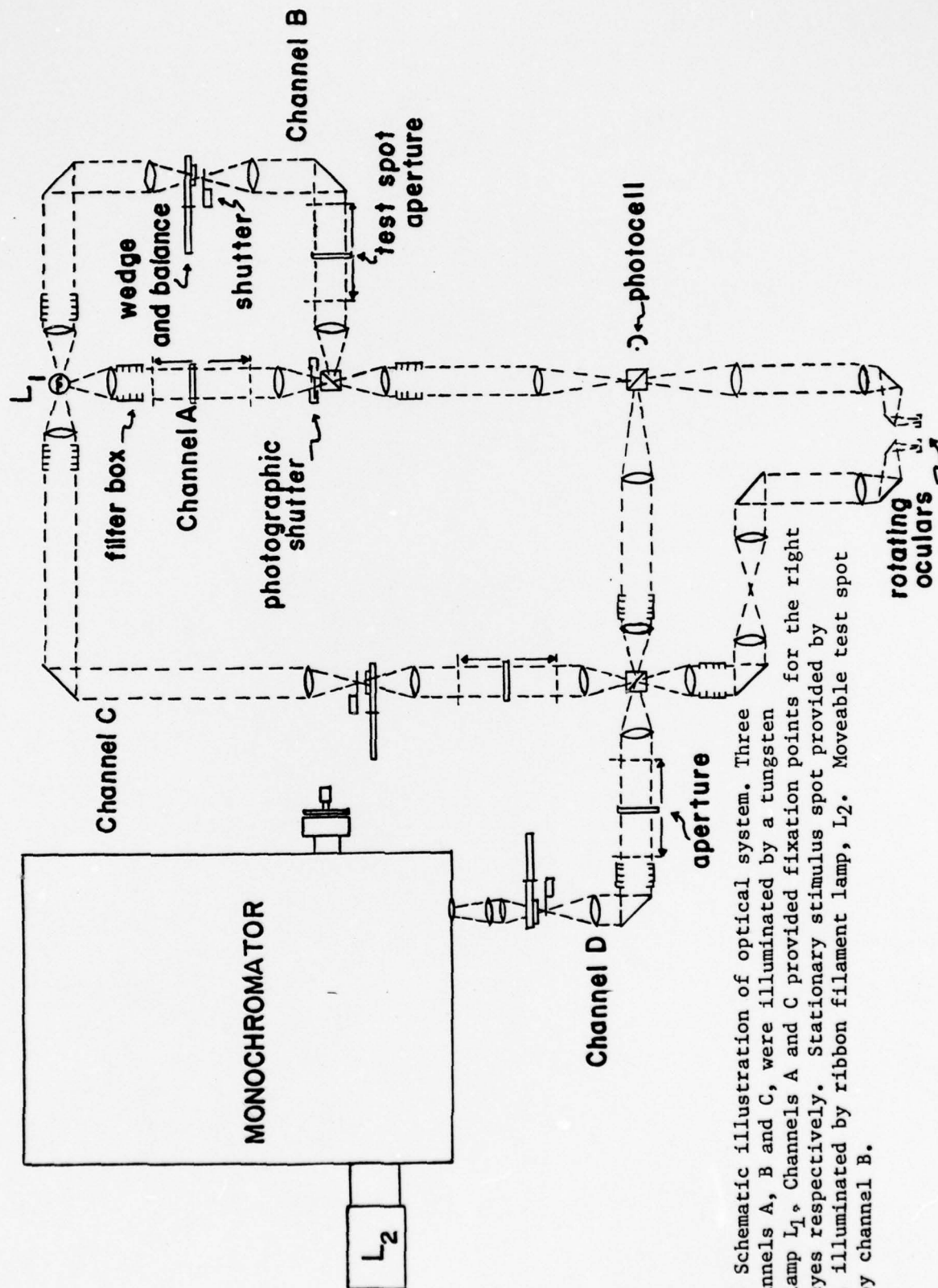


Figure 1. Schematic illustration of optical system. Three beams, channels A, B and C, were illuminated by a tungsten filament lamp L_1 . Channels A and C provided fixation points for the right and left eyes respectively. Stationary stimulus spot provided by channel D, illuminated by ribbon filament lamp, L_2 . Moveable test spot provided by channel B.

C were illuminated by a tungsten filament incandescent lamp operated at 6.3 amperes. Channel D was illuminated by a ribbon filament lamp through a Bausch and Lomb double grating monochromator. A stimulus spot of fixed luminance was presented via channel D. A test stimulus was presented via channel B. The monochromator illuminating channel D was set for maximum transmission at 575 nanometers. An interference filter with a peak transmittance at 575 nanometers was located in a parallel portion of the beam in channel B in order to match the illumination in channel D. Electrically actuated shutters (Uniblitz, Vincent Associates) permitted the presentation of 2-msec flashes of the stimulus targets. The flash duration and the temporal relation between the two flashes were controlled by a PDP-8 computer. Luminance control was achieved by circular Wratten neutral density wedges in channels B and D, each of which had a range of two density units. Additional adjustment of the luminance was achieved by the use of fixed filters; a device located in channel B permitted the motor driven insertion or withdrawal of two fixed filters of density 1 and density 2. Wedges in channels B, C and D were motor driven and coupled to continuous turn potentiometers which provided a varying voltage correlated with wedge position. Positions of the wedges and the two fixed filters in channel B were controlled by the computer. Field stops which defined the five minute stimulus targets were located in channels B and D. The stop in channel B was mounted in a special holder which could be placed in either of two positions under computer control.

The test spot field stops were so positioned that the spot in channel D was seen on a 45° meridian up to the left of the fixation point at a separation of 2° . The spot in channel B was seen either to the left or directly above the spot in channel D. The two spots thus defined either a horizontal or a vertical line, depending upon the position of the spot in channel B. The target holder in channel B rotated about an axis which coincided

with the position of the spot in channel D. The spot in channel B thus remained at the same distance from the spot in channel D when its position was changed. Limit switches on the target holder permitted the precise position of the spot either on a horizontal or a vertical line relative to the spot in channel D. The separation of the centers of the spots investigated in this experiment varied from ten minutes of arc to forty minutes of arc.

Pin hole stops defining fixation points were located in channels A and C. They were illuminated with red light through 2412 Corning filters and were approximately 30 secs of arc in diameter. Their luminances were adjusted so that they were fully visible to the dark adapted eye. The two fixation points were perfectly superposed in the right eye view and were thus seen as one. Only the fixation point in channel C was visible to the left eye. To a subject looking into the left and right oculars, a red fixation point was seen by the right eye and a red fixation point was seen by the left eye; the two points were easily fused so that a single fixation point was seen binocularly. A variable diameter aperture control in the final optical pathway to the left eye permitted occlusion of the stimulus spot from channel D without occlusion of the fixation point from channel C. The stimulus spot in channel D could thus be presented either to the right eye or to the left eye without altering the visibility of the fixation point seen by the left eye.

Calibration

The luminance in channel B was measured by a binocular matching procedure in which the right eye viewed a semicircular field which was seen adjacent to a semicircular matching field in a Macbeth Illuminometer viewed by the left eye. The Macbeth field was set to a known luminance and the two fields were matched by adjustments of the wedge in channel B. The

field in channel B, seen by the right eye, was then matched to an adjacent field in channel D, also viewed by the right eye. Finally, the field in channel D, seen by the left eye, was matched to the field in channel B seen by the right eye. A check on the relative luminance values measured for channel B, channel D seen by the right eye and channel D seen by the left eye was afforded by light detection threshold measurements made for each of these three conditions. The threshold measurements were in good agreement with the luminance matching data.

Shutter timing and stimulus onset asynchronies (SOA's) for the two flashes were checked with the aid of a photocell located at the last mixing cube in the right eye channel. Photocell output was displayed on a calibrated storage oscilloscope. The location of the test spot in channel B was adjustable relative to the position of the spot in channel D. Its precise position was controlled by a micrometer drive mounted on the target holder in channel B. Magnification of the system was such that a transverse distance of 0.1 inch in the test spot object plane subtended a visual angle of one degree.

PROCEDURE

Light detection thresholds were measured individually for the test stimulus spots in channels B and D using an ascending method of limits. Individual measurements were made for the various positions in which the channel B spot might appear. A minimum of ten determinations was employed for the calibration of average values. Individual determination of thresholds for the B and D spots were mixed randomly for a single session. For neither of the two observers was there any significant difference in light detection threshold for the stimulus spots as a function of their

position over the limited range of positions employed in this experiment.

In the main experiment, luminance of the test spot in channel D was set at a value of four times the light detection threshold value (0.6 log unit above threshold) for each observer. Under these circumstances, it appeared on each presentation at a relatively dim level with some fluctuation in brightness from trial to trial. The test spot in channel B was presented initially at a level approximately 0.3 log unit below light detection threshold in each threshold determination series. Within a series, for each succeeding presentation, the luminance of the test spot was increased by approximately 0.02 log unit. The stimulus presentations were initiated by the subjects themselves by depression of a button on a hand held control box. Subjects were instructed to respond to each presentation by signaling with the appropriate one of three response buttons: the two spots were arrayed horizontally, they were arrayed vertically, or their orientation could not be discriminated. In the last case, the computer reset the wedge to reduce density by 0.02 and after a four second delay, actuated a brief buzzer signal which indicated that the subject could initiate another stimulus presentation. This procedure continued until the subject pressed a response button signaling one or the other of the two orientations of the test spots. If the response was correct, a single buzzer signal was presented, wedge position at threshold was stored by the computer and after appropriate setting of the wedge and test spot position in beam B, a subsequent buzzer signal indicated to the subject that the next threshold series could be initiated. If the response was incorrect, the subject was so informed by two brief buzzer signals in quick succession, the wedge position was stored with an error notation and conditions were reset for another threshold determination. Conditions under

which errors were made were repeated randomly among succeeding threshold series.

The computer program was designed to adjust procedures for two important contingencies. First, if for any reason the subject signaled an orientation after the first flash in a given series, then the conditions were not accepted as representing a threshold and the initial wedge position for the SOA and target orientation conditions being tested was altered to increase the density by approximately 0.3 log unit for all succeeding threshold series under those conditions. If the number of flash presentations in a given threshold series prior to a correct response exceeded 30, the wedge density on the initial presentation was reduced by one half the range from the original value to the threshold value for all succeeding presentations of the same condition.

For any given experimental session, one spatial separation of the two test spots was investigated. In each session, seven different SOAs were employed. Three thresholds were determined for each of these asynchronies for each of the two orientations. Thus, there were 42 threshold determinations in each session. Time required for each session was approximately one and one-half hours. SOAs varied from -420 msec, with the suprathreshold test spot in channel D preceding the spot in channel B, to 490 msec with the spot in channel B preceding the fixed luminance spot. A total of 14 SOAs was investigated at 70 msec intervals from -420 to +490. It was arbitrarily decided to obtain data for only half of the SOAs in a given experimental session so that each threshold determination could be replicated three times per session. The median of the three determinations was taken as representative of threshold for that session. In each session, seven SOA values at 140 msec intervals were employed either from -420 to +420 msec, or from -350 to +490 msec. Two experimental sessions were conducted with each of four spot separations

and each of the two series of SOAs. The full experiment called for sixteen sessions for each of the two subjects. Complete data were not obtained for the ten minute spot separation, however. Subject JLB had great difficulty resolving orientation in most sessions with the ten minute spot separation. The variability of his data was too great for these results to be usable. Subject IMK was able to obtain repeatable results for the ten minute spot separation but data were lost for one session at this separation with the +70 msec SOA by reason of a programming error.

A second experiment was performed in which the stimulus spots were presented haploscopically. The spot in channel D was presented to the left eye, while that in channel B was presented to the right eye. The red fixation points presented to the two eyes were readily fused so that stimulus geometry was identical to that for the monocular presentations. Only one test spot separation was employed, 30 minutes of arc. The purpose of this experiment was to determine whether the effects observed with a monocular stimulus presentation would persist under conditions where neural events triggered by the individual stimulus spots would be expected to interact only at a cortical level. Two sessions were obtained for each of the two subjects with each of the two SOA sequences as in the main experiment. Prior to all experimental sessions, subjects were dark adapted for at least twenty minutes.

RESULTS

The results of the main experiment are presented in Figure 2 for each of the two subjects. Data are plotted in terms of luminance in log microlamberts as a function of SOA for each of the stimulus spot separations for which results were available. Each of the points represents an average of

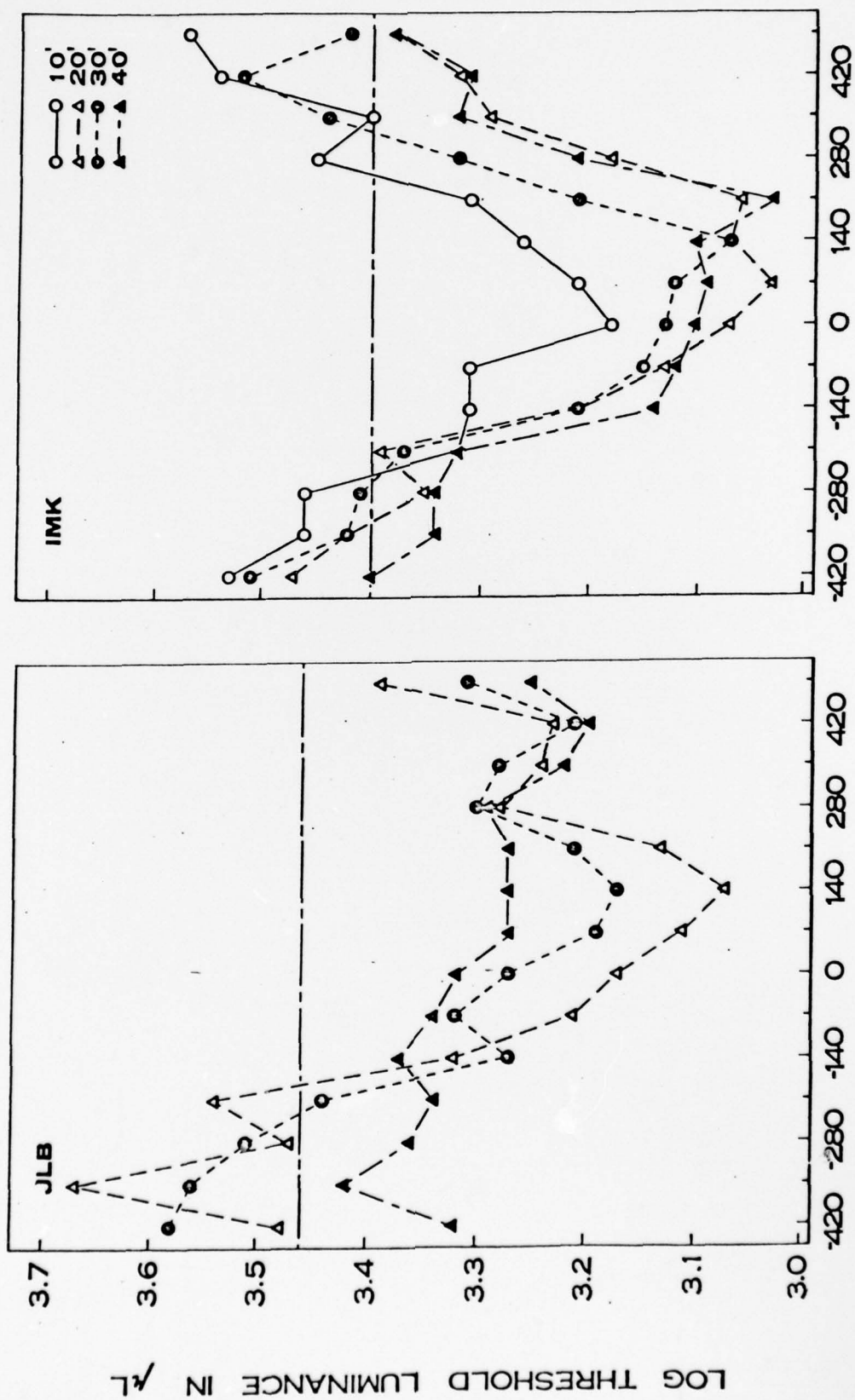


Figure 2. Test spot threshold luminance for orientation discrimination as a function of stimulus onset asynchrony (SOA). Negative values represent delay of the test spot relative to the fixed luminance spot. Four separations of the stimulus spots are identified by symbols. Subjects JLB and IMK.

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the median values for both sessions for both of the stimulus orientations after the application of an adjustment for day to day variability. There were some overall shifts in threshold from one day to another and failure to adjust for this would have resulted in a misleadingly irregular appearance of some of the curves in Figure 2 by reason of the investigation of alternate SOA values on different days. Accordingly, an average threshold value was calculated for each session, along with an overall sessions average for a given spatial separation. Individual values in each session were then adjusted by an amount equal to the difference between these two averages before the averages across sessions for a given SOA value were calculated.

The horizontal dash-dot line across each subject's half of the figure represents the light detection threshold. The luminances represented in Figure 2 are the threshold luminances of the test spot in channel B for correct identification of the orientation of the two spots as either vertical or horizontal. The most striking aspect of the results is the fact that luminance threshold for orientation discrimination appears to be systematically lower over much of the range of SOAs than is the light detection threshold. The lowest threshold values appear to occur in the vicinity of SOAs of +70 to +140 msec. There is a suggestion that at extreme SOA values, thresholds may be higher than the light detection threshold, but the differences are small and inconsistent for the two subjects.

The results for the two subjects differ in several ways. Thresholds for IMK reach somewhat lower levels than those for JLB over the range of SOAs from -140 to +210 msec. On the other hand, thresholds for IMK are consistently higher for SOAs from +350 to +490 msec. The data for JLB show two minimum threshold values for the functions presented, one at an SOA of 140 msec and one at an SOA of 420 msec. The maximum value

between these two minima is remarkably consistent for all three spatial separations represented. In the data for JLB, the minimum threshold appears to be related to the spatial separation of the stimulus spots; the closer the spots, the lower is the threshold. However, results for JLB with the ten minute separation, although highly variable, suggest that threshold for this separation is somewhat higher than threshold obtained for the forty minute separation. In the data for IMK, the functions for separations of twenty minutes and forty minutes are quite similar. Data for the thirty minute separation rise more quickly with increasing SOA values beyond 104 msec. The data for the ten minute separation represent the highest threshold values of all.

Statistical Analyses

The data were subjected to several statistical analyses. An analysis of variance was performed independently on the data for each of the two subjects. For the purpose of these analyses, data for adjacent pairs of SOA values were pooled. This procedure eliminated any confounding of day to day shifts in overall threshold level with SOA. The classifications employed were SOA blocks (B), spatial separation (S) and stimulus orientation (O). Results of these analyses are presented in Table I in terms of the chance probability of the results. The influence of SOA on threshold is highly significant for both subjects. Spatial separation of the test spots is highly significant for IMK, but not significant for JLB. Although the functions for different separations are dissimilar for JLB, the average threshold values over SOA are quite similar for the three separations investigated. In the case of IMK, the functions for three of the separations are similar in form, but differences in the overall threshold values for the different separations are apparently sufficient to render the spatial separation of test spots a highly significant classification.

TABLE I

Results of an analysis of variance of threshold data for subjects JLB and IMK for classifications of stimulus onset asynchrony blocks, spatial separation and stimulus orientation. Table entries represent probability for chance occurrence of calculated F ratios.

	<u>JLB</u>	<u>IMK</u>
SOA Blocks (B)	.000	.000
Spatial Separation (S)	.697	.000
B x S	.016	.692
Stimulus Orientation (O)	.039	.006
B x O	.377	.350
S x O	.671	.037
B x S x O	.856	.095

On the other hand, the different form of the functions for different separations is associated with a significant interaction between SOA and separation for JLB. This interaction is not significant for IMK. The orientation of the stimulus spots proved to be significant for both observers, at a slightly lesser level for JLB than for IMK. An examination of those conditions for which errors were made revealed a substantially greater number of errors for horizontal positioning of the stimulus spot for IMK and a slightly greater number of errors for the vertical position for JLB. Luminance thresholds were higher for the horizontal position for IMK and for the vertical position for JLB. These results may reflect slight astigmatic conditions in the two observers, or simply response biases. The interaction between stimulus orientation and SOA was not significant for either observer. The interaction between orientation and separation was significant for IMK, reflecting a substantially greater difference in threshold for horizontal and vertical orientations for the two wider separations than for the ten and twenty minute separations of the test spots.

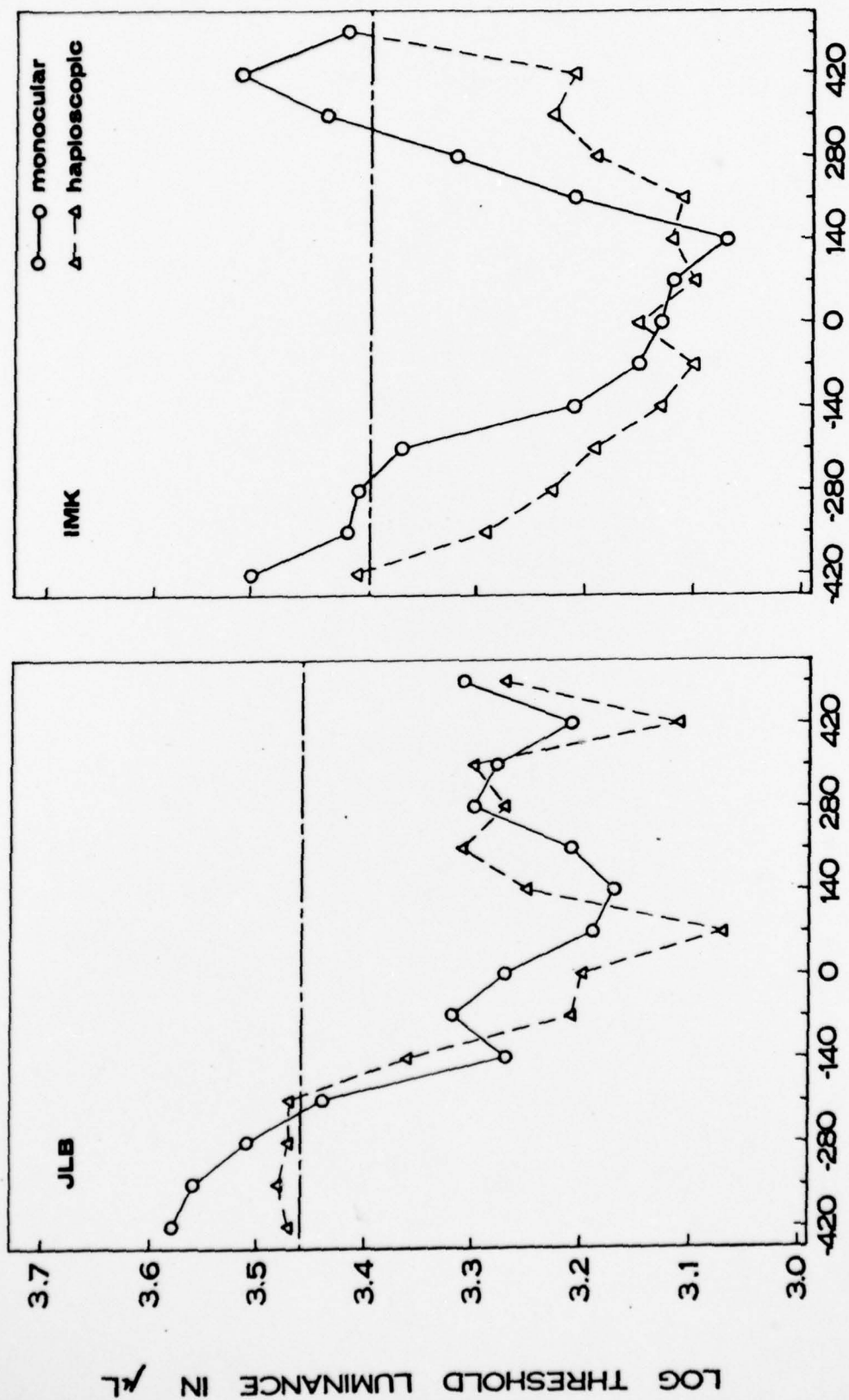
The apparent deviation from an SOA of zero of the minimum threshold in the data of Figure 2 indicates that the test spot for which luminance threshold was being determined, the dimmer of the two spots, must be presented ahead of the fixed luminance spot for minimum threshold. This finding, if correct, is of importance in the interpretation of these results. In order to test the statistical significance of this deviation from zero SOA, a procedure described by Williams (1959) was employed. A polynomial equation was fitted to the function in Figure 2 for each of the subjects. The differential of the fitting equation was then set equal to zero in order to define maxima and minima. William's procedure permits definition of the limits of the differential, based on the variance of data from which the fitting equation is determined, within which a minimum or maximum value may be expected at various chance levels.

On the basis of this analysis, the deviations from zero to the minima for JLB were significant at the 1% level of confidence for both the twenty minute and thirty minute separations. The forty minute function for JLB in Figure 2 does not provide sufficient definition of the minimum value for the technique to be applied. The best reasonable fit of this function is a straight line of negative slope. The function is thus in accord with the conclusion that threshold values are lower when the dimmer stimulus spot precedes that of fixed luminance.

In the data of IMK, displacement of the minimum threshold toward a positive SOA value was statistically significant at the 1% level for separations of twenty and forty minutes and at the 5% level at a separation of 30 minutes.

Haploscopic Study

The results of threshold determinations with the variable luminance spot presented to the right eye and the fixed luminance spot presented to the left eye are shown in Figure 3. Only the thirty minute separation was employed. Both subjects showed a decrease in threshold similar to that shown for the monocular data and in the same SOA range. The two minima which are shown in the monocular data for JLB are also found with this procedure, along with the substantially higher thresholds for negative SOA than for positive SOA values. The results for IMK are more symmetrical with respect to SOA than the results for JLB as was the case with her monocular data. The haploscopic results differ from the monocular in showing a broader region of SOA values in which threshold is substantially lower than the light detection values, but the minimum threshold values are remarkably similar to the haploscopic and monocular conditions. The qualitative results obtained monocularly are



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Figure 3. Same as figure 2, but for 30-minute stimulus separation only with test spot presented to right eye, fixed-luminance spot to left eye. Monocular data for 30-minute separation from Figure 2 are included for comparison.

replicated haploscopically, both with respect to the general finding of lowest threshold in the middle region of SOA values and with respect to those characteristics of the results unique to each of the individual subjects.

Method of Constant Stimuli

An additional experiment was carried out to determine whether the result was dependent on the psychophysical method employed and to examine the slope of the frequency of seeing function for orientation discrimination thresholds. Light detection thresholds were redetermined for JLB and two additional subjects with the method of constant stimuli. Two spots separated by 30 minutes were then presented with one suprathreshold by 0.6 log unit as before and the other at each of 3 luminances ranging from the light detection threshold to a luminance 0.4 log unit lower. Only two SOA's were employed, -350 and +140 msecs. These were selected as representative of the maximum difference in threshold found in the original experiment (Figure 2). A forced -choice procedure was used; subjects were required to choose either "horizontal" or "vertical" after each stimulus presentation.

Results were the same for all three subjects. The light detection threshold based on 50% affirmative response in the constant stimulus procedure was approximately equal to the orientation discrimination threshold for an SOA of -350msecs. The orientation discrimination threshold for an SOA of +140 msecs was significantly lower. The results for JLB are illustrated in Figure 4. The original results are thus confirmed with a different procedure and with two additional subjects. It is of interest to note that the slope of the function for the lower threshold, +140 msec SOA, is less than that for the higher threshold, -350 msec SOA. This was true for all three subjects.

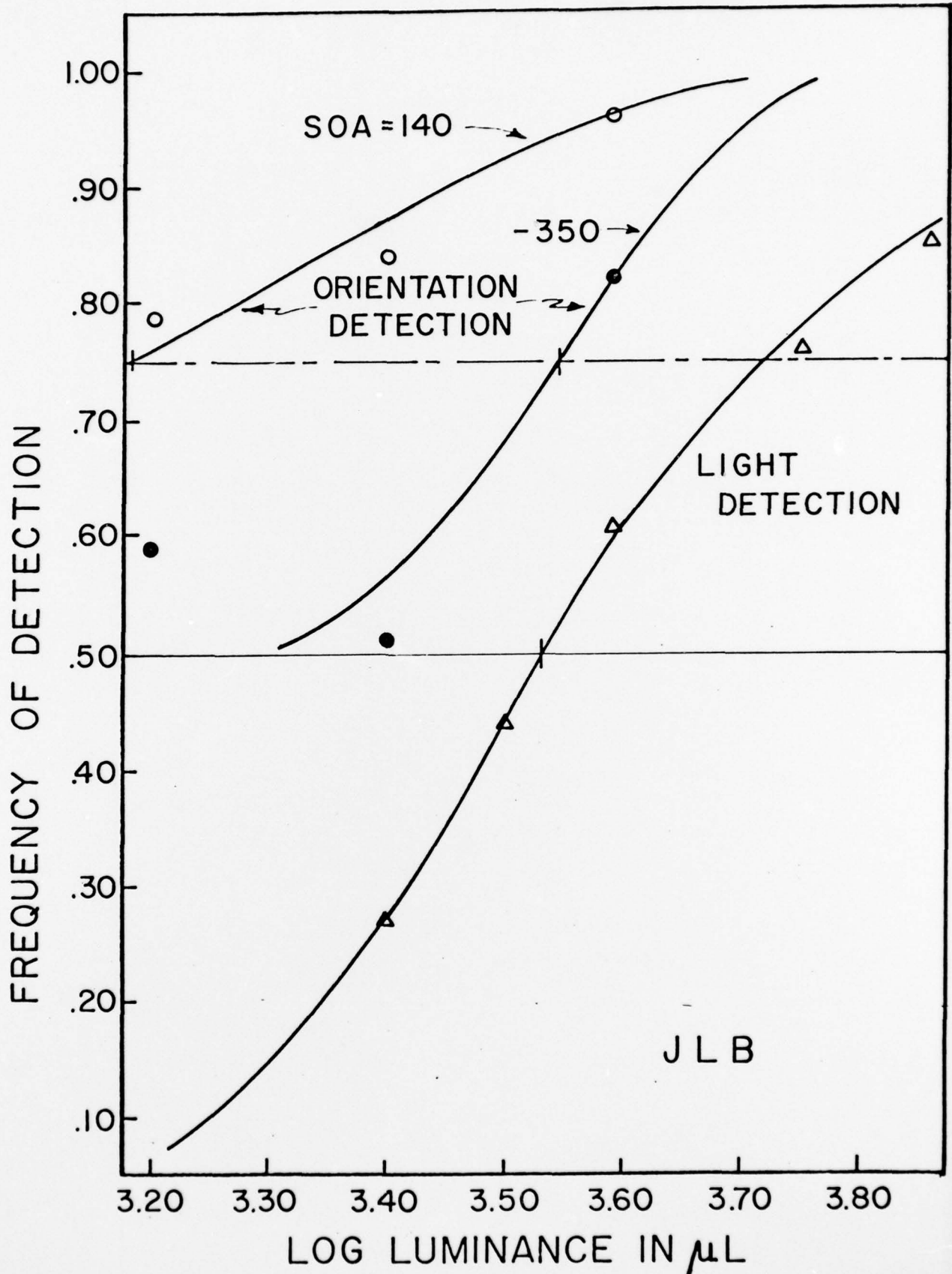


Figure 4. Frequency of light detection or of correct detection of orientation as a function of the logarithm of test spot luminance. Stimulus onset asynchronies of -350 and +140 msec. Subject JLB.

DISCUSSION

The results of this experiment suggest that information concerning the brief illumination of a small region of the retina may be utilized more effectively when that illumination occurs in conjunction with stimulation of an adjacent region. The spatial orientation of two test spots in the visual field can be discriminated reliably when one of the spots is illuminated at a level below that required for its detection in isolation. This effect is optimum when a low luminance test spot for which a threshold value is being determined precedes by from 70 to 200 milliseconds a stimulus spot of fixed luminance at approximately four times its light detection threshold level. One possible implication of this result is that the interpretation of the visual stimulus depends upon a cortical process which utilizes information from multiple retinal stimulation most effectively when resulting cortical events occur simultaneously. Thus, lower luminance stimulation, which is associated with a longer delay between retinal excitation and the subsequent resulting cortical activity, must precede high luminance stimulation by a compensating amount of time. An interval of approximately 140 milliseconds is a reasonable amount of time under the circumstances. A stronger argument for dependence of the effect on a cortical process is provided by the replication of results with haploscopic stimulation. The lowered threshold can not be attributed to retinal interaction effects under these circumstances.

A level of retinal stimulation which is insufficient to elicit a threshold for light detection may nonetheless result in the propagation of a neural signal to some region of the visual cortex. Although such a signal in isolation might not give rise to any conscious result, when it occurs in conjunction with another somewhat stronger signal which stimulates a proximal region, a conscious perception of the two stimuli and their spatial relation results.

There is a continuing debate as to the minimum number of quanta which

must be absorbed by retinal receptors for a stimulus to be consciously perceived. It has been widely accepted for some time (Hecht, Shlaer and Pirenne, 1942) that between five and seven quanta are sufficient to produce sensation, although others have argued that as few as two may be sufficient (Bouman, 1959). An argument favoring the larger number of quanta has been linked to the advantage this would afford in eliminating confusion from spontaneous retinal activity. Breakdown of individual rhodopsin molecules in the retina occurs spontaneously, but these events don't seem to result in spurious visual sensations.

An important element in this debate is the nature and stability of the criterion of threshold which a subject employs for detection of a visual stimulus. In complete darkness with no physical stimulation of the retina, one becomes aware of faint visual sensations which have no correlation with light stimulation. Such spontaneous effects and those resulting from stimulation can't be discriminated with confidence at low levels of physical stimulation. With forced choice procedures, however, subjects are able to detect very low levels of physical stimulation at significantly better than chance levels.

Sakitt (1972, 1976) has argued for the adequacy of a single quantum for stimulation of the visual system. She has demonstrated that under circumstances where subjects are very uncertain as to the presentation of a test flash, their ratings of the probability of presentation in each of several possible intervals are significantly better than chance (Sakitt, 1976). There is thus evidence that information is transmitted from retina to cortex under circumstances in which subjects are unwilling to accept the resulting effect as positive with respect to some threshold criterion in an ascending method of limits experiment.

In our experiment, when those stimulus spots which were subthreshold with the criteria of threshold we adopted for light detection were presented in conjunction with another suprathreshold stimulus spot in the right temporal relation, they were very often readily discriminable. The criteria of threshold were obviously different for light detection and orientation discrimination, but neither procedure involved forced choice. Criteria for threshold orientation discrimination were fairly stable. Subjects were encouraged to respond if they had any inclination of the correct orientation. Under these conditions, IMK recorded a total of 20% errors and JLB recorded a total of 16% errors. The criteria of threshold adopted produced responses which were correct well above a chance level. Thus, under appropriate SOA conditions, a test flash luminance which was almost never associated with a positive light detection response was associated with discrimination of orientation of two stimulus spots on a high percentage of presentations.

In the later experiment when a forced choice technique was employed in orientation discrimination, the same facilitation effect was clearly shown for the +140 msec SOA. We conclude that the effect is not in some way an artifact of our psychophysical method. The less steep slope of the frequency of seeing function for the lower threshold, + 140 msec SOA condition as compared to the -350 msec condition, is in accord with the idea that fewer quanta are required at threshold (Hecht, Shlaer and Pirenne, 1942).

It is of interest to speculate what the mechanism for this effect may be. Both the nature of the SOA under optimum conditions and the replication of the effect haploscopically argue for a cortical locus of the mechanism. It is possible that cortical cells which respond much more vigorously to line stimuli than to point stimuli provide a basis for summation of any stimulus elements presented on the retina as long as these elements lie along the appropriate line. The visual acuity for detection of a dark line against a light background is

remarkably high. A line subtending a visual angle of less than one second of arc can be discriminated if it is sufficiently long. A short line segment or a black spot with a diameter equivalent to the line width could never be detected. The explanation of this type of visual acuity must rest with some sort of summation process occurring in the cortex where a cell or cells receive converging signals from two or more retinal ganglion cells, the receptive fields of which are arrayed along the line of retinal stimulation.

Alternatively, as was suggested to us by H. R. Blackwell (personal communication), the suprathreshold spot may serve to focus attention on the region of the visual field involved, or to enhance for a brief interval the sensitivity of cortical mechanisms which serve that region. The facilitation effect then would not depend upon having the suprathreshold spot and the facilitated spot both involved as elements in the discrimination of orientation. The suprathreshold spot would serve merely as a cueing signal.

In order to test this possibility, the stimulus pattern was changed. The suprathreshold spot was presented in the same location and at the same luminance. Two additional five-minute spots were presented. The first of these was on the same 45° meridian as the suprathreshold spot, but 30 minutes further away from the fovea. The second was 30 minutes away from the first, either horizontally to the left, or directly above. These two spots were always presented simultaneously and at the same luminance, either 140 msec before or 350 msec after the suprathreshold spot. It was assumed that if the effect we have found can be explained as a kind of attentional effect or cueing effect of the suprathreshold spot, not specifically dependent upon orientation discrimination, then the threshold luminance for discrimination of the orientation of the two more distant spots might be influenced by their temporal relation to the suprathreshold spot; the facilitation effect should be found with a + 140 msec SOA. This proved not to be the case. Threshold luminance for discrimination of the

orientation of the two spots was approximately equal to their individual light detection thresholds at both SOA's.

Another possible mechanism which occurred to us was one involving cortical motion detectors. When two light spots at an appropriate separation are presented at the proper time interval, there may be the perception of motion. If specialized cortical cells are aroused by such stimulation, their activity might enhance the detection of the orientation of two spots. The subject might not see two spots clearly but would be aware of motion in a given direction and the direction of motion would define the orientation of these spots. The conditions under which minimum thresholds were found in the present experiment did not produce any significant apparent motion. Apparent motion was reported for larger SOA's, however, at near threshold levels. Therefore, movement discrimination mechanisms do not seem to provide a likely explanation of the results. We conclude that the facilitation effect may indeed depend upon some mechanisms involving cells that respond to specific stimulus orientations.

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